



Genetic linkage map construction for fibre quality traits in intraspecific upland cotton (*Gossypium hirsutum* L.)

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Abstract

The quantitative traits such as fibre length, fibre strength, fineness, uniformity, color and elongation are considered as important fibre quality traits fetches high market price for cotton, thus identification of quantitative trait loci (QTL) for fibre quality traits in cotton (*G.hirsutum*) would be beneficial for cotton fibre yield and quality improvement. Hence the main objective of this study was to identify QTLs for fibre quality traits using an intraspecific mapping population derived from a cross between JKC737 (*G.hirsutum*) and JKC725 (*G.hirsutum*) comprising 180 F₆ – RILs. Population study was carried out for 3867 primer pairs using two parental genotypes (JKC737 & JKC725) of a mapping population developed for fibre quality related traits; only 174 SSR were polymorphic. Owing to a low level of polymorphism between the parental genotypes and a high degree of segregation distortion in recombinant inbred lines, genotypic data of only 120 polymorphic SSR on the mapping population consisting of 180 RIL could be used for construction of a linkage map; 120 SSR loci were mapped on eighteen different linkage groups that covered a total genetic distance of 2883.8cM. Hopefully this map will be enriched with more SSR loci in future and will prove useful for identification of quantitative trait loci/genes for molecular breeding involving improvement of fibre strength and other related traits in cotton.

Keywords: QTLs, fibre quality traits, genetic linkage map, marker assisted selection, RIL, polymorphic primers

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INTRODUCTION

Improving cotton fibre quality is a major breeding goal for upland cotton in India. The advancement in molecular biology provides new approach like genomics to construct molecular map of key traits that will reveal genetic architecture of traits and helps in the marker assisted selection (MAS) for cotton improvement. Using DNA markers in MAS can untether direction towards robust crop improvement (Burr *et al.* 1983, Tanksley *et al.* 1988, Xu and Crouch 2008) especially complex traits like fibre quality (Kohel *et al.* 2001) through indirect selection of target traits.

Genetic mapping and marker-assisted breeding in all crops require a suitable marker system with increased throughput, decreased cost per data-point and best map resolution (Kumar *et al.* 2007; Gupta *et al.* 2008). The drafted genome of tetraploid cotton (*Gossypium hirsutum*) has just been published, overcoming the sinister task of quality assembly due to highly homologous subgenomes (Li *et al.* 2015, Zhang *et al.*

2015). Sequencing initiative of *G. hirsutum* waited for a long time due to large genome size (2.5 Gb) and huge amount of (~80%) repetitive sequences (Hendrix and Stewart 2005). Most of high-density interspecific linkage maps (Fang and Yu 2012, Rong *et al.* 2004, Yu *et al.* 2011, Zhao *et al.* 2012) and intraspecific linkage maps have been developed in cotton. Adding to that, so many QTL mapping studies for fibre quality and yield have been conducted with both interspecific (He *et al.* 2007, Lacape *et al.* 2005, 2010, Mei *et al.* 2004, Yu *et al.* 2013) and intraspecific populations (He *et al.* 2011, Liu *et al.* 2012, Qin *et al.* 2008, Shen *et al.* 2006, Sun *et al.* 2012, Ulloa *et al.* 2005, Wang *et al.* 2006, Wu *et al.* 2009, Zhang *et al.* 2005, 2009, 2012). All those studies contribute more to understanding of complexity of genetic control of cotton fibre quality and yield.

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Microsatellite DNA markers has been most widely used, due to its ease of use by simple end-point PCR and to high degree of information provided by its large number of alleles per locus (Kumar *et al.* 2009). Researchers developed SSRs to identify markers correlated with important quality traits; such as fibre yield and quality (Zhang *et al.* 2005). Chee *et al.* (2004) highlighted utility of *G. arboreum* EST sequences in Genbank database for developing PCR-based markers targeting known function genes in cultivated tetraploid cotton. Kumar *et al.* (2006) demonstrated that searching cotton ESTs in BLAST against Arabidopsis database is both feasible and practical for predicting location of introns in cotton ESTs. Han *et al.* (2004), Qureshi *et al.* (2004) and Park *et al.* (2005) demonstrated EST-SSR markers as a cost-effective strategy for cotton by exploiting EST databases that would facilitate the development of a high-resolution integrated genetic map of cotton for structural and functional study of fibre genes and fibre quality marker assisted selection. Abdurakhmonov *et al.* (2008) highlighted that SSR and EST-SSR markers associated with fibre development traits have the potential to play a key role in understanding of cotton fibre development and also for development of superior cotton cultivars through marker assisted selection programs.

MATERIALS AND METHODS

Plant Materials Used and Experimental Conditions

Two genotypes of *G. hirsutum* (superior JKC725 and inferior JKC737) with respect to fibre quality are used in this study. These cotton varieties are parents of two mapping population developed at R&D Centre, JK Agri Genetics Ltd, Ravalkol, Hyderabad during 2013-2014. The intraspecific mapping population (RIL) of cotton was also generated at the same location.

Briefly, for the generation of intraspecific recombinant inbred lines (RIL) two *Gossypium* genotypes contrasting for fibre quality traits JKC737 and JKC725 were crossed and the resulting F₁ plant was self-pollinated to obtain the F₂ offspring that were further self-pollinated and advanced to F₆ generation using single seed descent method to obtain RILs. An intraspecific mapping population comprising 180 RILs was used for construction of linkage map and further for QTL analysis.

DNA Isolation

Leaf samples of two different genotypes (JKC737 & JKC725) of *G. hirsutum* were collected from Ravalkol, Hyderabad. Fresh or frozen leaf tissues of cotton plants were used for DNA extraction. Fresh tissue quickly frozen in liquid nitrogen gave satisfactory yields up to 3 months of storage. The protocol was standardized for 2 g samples that can be handled in a 50 ml disposable screw capped tube, while similar conditions on mini

scale using 0.2 g tissues can be scaled down and easily fit into an eppendorf tube. DNA was extracted by modified CTAB extraction method and the DNA concentration and purity of each sample were measured with a UV-Vis spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE). Quality of DNA was checked in agarose gel electrophoresis.

Analysis of RILs with Polymorphic SSRs

Genomic DNA of 180 samples from JKC725 and JKC737 were first screened with SSR markers to identify polymorphic markers between the two mapping parents. Primer sequences for SSR markers are available from the Cotton Microsatellite Database. RILs were developed after F₆ generation to get uniform and pure homozygous population. In most cases alleles are distributed in the RIL population in a 1:1 ratio.

A total of 3867 SSRs were used to get the polymorphic primers between the two genotypes of *G. hirsutum*. A total of 174 SSRs were found to be polymorphic. Majority of SSR primers are having a band size of 200bp to 300bp. However, when we ran all the SSRs against the RIL population, 54 SSRs showed segregation distortion (i.e., didn't follow the Mendelian segregation ratio 1:1) accompanied by more than 20% heterozygosity. Those SSRs are removed from further analyses.

Construction of Linkage Map

Linkage map was constructed with the help of **MAPMAKER3** from RIL population generated in our R&D field at Hyderabad. A total of 120 SSRs were used for construction of map. The dataset was prepared in excel spreadsheet and uploaded in MAPMAKER for assignment of SSRs in different linkage groups (at min LOD 3.00, max Distance 50.0). Eighteen groups were generated and few SSRs did not make any groups, and the number of SSRs in each group varies from 2 to 13.

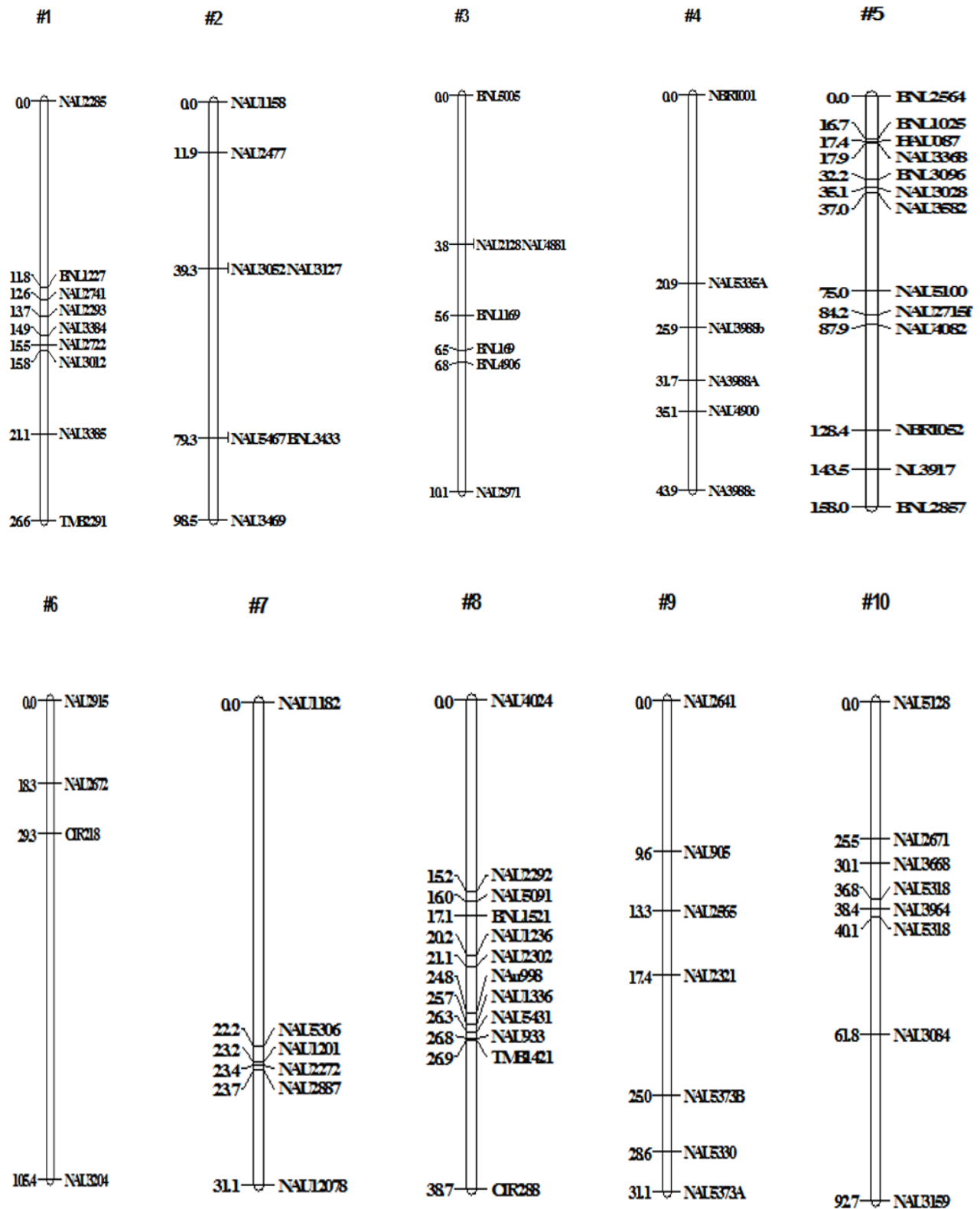


Fig. 1. An intraspecific genetic linkage map of *G. hirsutum* based on RIL mapping population generated by crossing *G. hirsutum* (JKC737 x JKC725). The map of 18 linkage groups were generated with 120 polymorphic genomic SSR markers using MAPMAKER3 at min LOD 3.0 max Distance 50.0

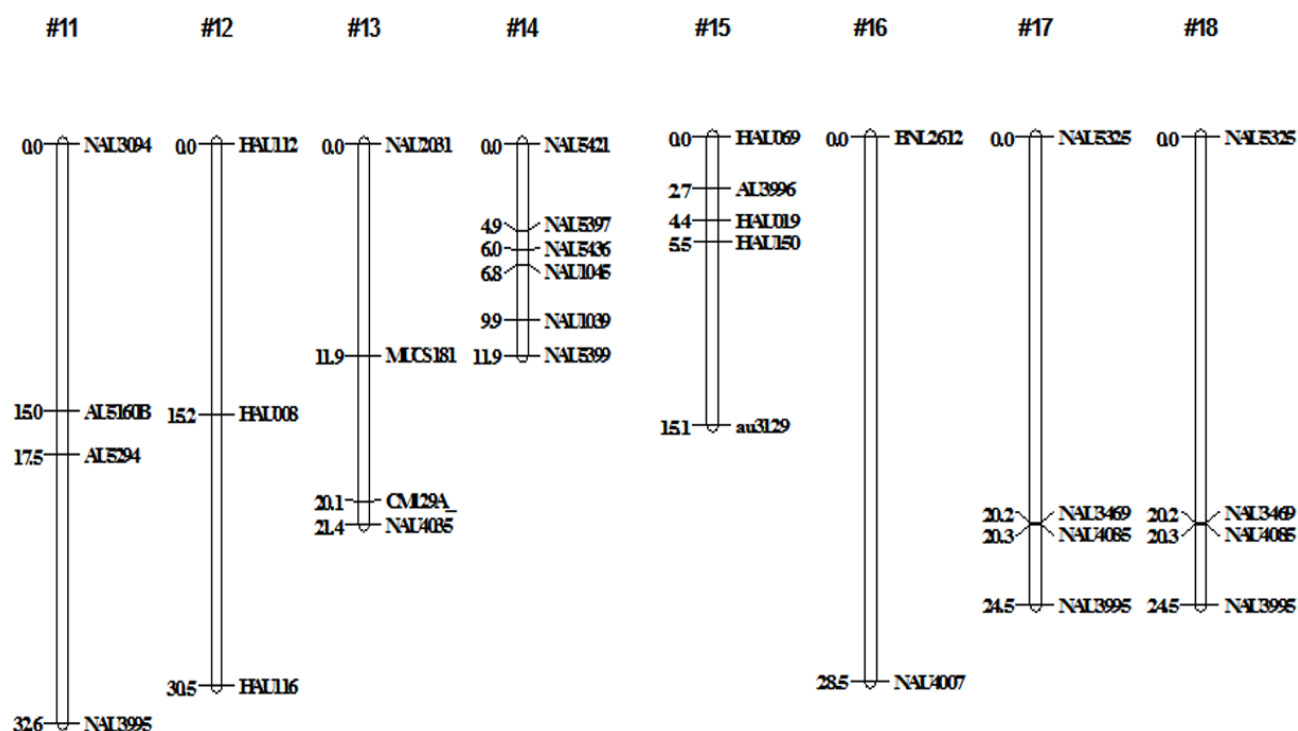


Fig. 1 (continued). An intraspecific genetic linkage map of *G. hirsutum* based on RIL mapping population generated by crossing *G. hirsutum* (JKC737 x JKC725). The map of 18 linkage groups were generated with 120 polymorphic genomic SSR markers using MAPMAKER3 at min LOD 3.0 max Distance 50.0

RESULTS AND DISCUSSION

Cotton marker-assisted selection programme is currently focused on introgression a fibre quality QTL from a *Gossypium hirsutum* cultivar (JKC725, which produces a very strong, long thin fibre) into a *Gossypium hirsutum* cultivar (JKC737 early and high yielding). QTLs underlying good fibre quality traits were located in and around 17 different chromosome segments on cotton genome map. Breeders hope to enhance intrinsic fibre quality of JKC725 through the accumulation of these fibre quality-associated QTLs from JKC737. A total of 120 polymorphic markers were used to construct 18 Linkage groups covering a total of 2883.8 cM.

Opportunity for improve our understanding of genetic variability and structure of *G. hirsutum* genome, a comprehensive PCR-based marker linkage map for fibre quality that covered 70.6% of upland cotton genome was constructed. Recently Zhang *et al.* (2012) developed a crossing population in upland cotton and constructed a genetic map covered 4184.4 cM, and that approximately spanning 94.1% of the complete tetraploid cotton genome and having 978 simple sequence repeat (SSR) loci. A drafted physical map of D-genome cotton species (*Gossypium raimondii* Ulbr., D5) has been completed and *G. hirsutum* genome is being sequenced, which gives functional markers and SSR markers for construction of genetic linkage map and QTL mapping for fibre quality traits to facilitate MAS. In the present study, a genetic map was constructed using an RIL

population derived from an upland cotton hybrid and used for tagging cotton fibre quality in upland cotton.

The occurrence of segregation distortion in plants is very common, a process in which genotypic frequencies are skewed from expected violating Mendelian segregation ratios and these deviations can't be evaluated by simple genetic methods (Li *et al.* 2010, Lu *et al.* 2002, Song *et al.* 2005). Segregation distortion is widespread in intra and interspecific crosses (Causse *et al.* 1994, Lacape *et al.* 2009, Rong *et al.* 2004, Ulloa *et al.* 2002, Yu *et al.* 2011, Zhao *et al.* 2012), and is driving force in evolution of species (Taylor and Ingvarsson, 2003). Mangelsdorf and Jones (1926) reported for first time occurrence of segregation in maize, using morphological markers and afterward McCouch *et al.* (1988) and Pereira *et al.* (1994) reported segregation skewness in rice, sorghum, and tomato. Many factors like pollen tube competition, pollen killer genes, selective fertilization, abortion, chromosome translocation etc., are major causes of segregation distortion (Li *et al.* 2007, Luo and Xu 2003, Taylor and Ingvarsson 2003, Zhu *et al.* 2007).

In this study, genetic map of cotton is developed from JKC737 x JKC725 which will serve as vital genomic resources for fine positioning of important traits, genome organization and function, map-based gene cloning, comparative genomic analyses in cotton. MAS studies unveil that upland cotton has narrow genetic base resulting into low rate of polymorphism among them

(Gutierrez *et al.* 2002, Saha *et al.* 2003, Wendel *et al.* 1992, Van Esbroeck *et al.* 1998). For the efficient utilization of genetic resources from cotton molecular breeding approaches need to be established. This requires better understanding at genomic level which is the key feature. It is therefore a dire need to construct genetic linkage map between upland cotton.

Out of 3867 SSR primer pairs tested, 174 SSR primers (3.5%), detected polymorphism between two genotypes. The polymorphic band size varies from 150bp to 275 bp. In some SSRs more than two polymorphic bands were also found between the two genotypes. More than two alleles were detected with most of the primers, and only polymorphic alleles were considered. The fact that we detected more than two alleles in many SSRs indicates the tetraploid origin of *Gossypium hirsutum*. The allele sizes varied from 100 bp to 400 bp. Most of the SSR primers are bi, tri, tetra and hexanucleotides. A similar low level (2.97%) of SSR polymorphism was reported by Wang *et al.* (2006) who tested 4106 markers in a *G. hirsutum* RIL population for QTL mapping of fibre quality traits.

Out of 174 polymorphic primers 120 polymorphic primers followed the Mendelian segregation in F6 RIL population. A basal level of heterozygosity has been detected in most SSRs with an average of 8.4%. So the population has not yet become fully homozygous. May be another two or three generations is needed for getting 100% homozygous population. This may be due to the polyploidy nature of this species.

Skewed segregation ratios have been reported frequently in cotton (Lacape *et al.* 2003, Mei *et al.* 2004, Ulloa *et al.* 2002, 2005). High frequency of segregation distortion (49–80%) has been observed in inter-specific crosses, most likely due to divergence between species

(Paterson *et al.* 1988). The frequency of distorted ratios was observed in this study. Total 54 SSR primers were discarded due to this distortion.

From linkage map it was found that except 10 SSRs remaining 110 SSRs are distributed in 18 different linkage groups. Group no. 3,6,8,9,11,12,13 shows similarity with previous results. Group 14, 15 and 16 are newly formed group having no similarity with previous results. But group no.1,2,4,5,7,10,17 and 18 are ambiguous and consists of both type of chromosomes if compared with previous results. With the help of above linkage map QTLs can be identified for fibre quality in cotton. . In addition to conventional breeding methods, cotton breeders have access to new biotechnology tools such as marker-assisted selection which enable them to create new cotton varieties that are higher yielding and generate a better quality fibre. Varieties can thus be screened directly on the basis of genotype, i.e. from genes contained in the genome, contrary to conventional breeding strategies based on phenotype (physical manifestation of a trait in a plant induced by expression of specific genes).

Understanding the molecular genetics of genome cotton can be important for many reasons. They can foremost serve as a simple model system to study complex quantitative traits, yet only a limited number of genetic maps and QTL studies have been conducted. There is a significant opportunity for further mining the diploid genome with efficient marker systems to facilitate genetic mapping of fibre genes. In the present study, we used SSR markers to generate a framework genetic map of cultivated diploid cottons. The genetic map was used to identify QTL linked to fibre traits.

REFERENCES

- Abdurakhmonov IY, Kohel RJ, Yu JZ, Pepper AE, Abdullaev AA, Kushanov FN, Abdurakimov A (2008) Molecular diversity and association mapping of fibre quality traits in exotic *G. hirsutum* L. germplasm. *Genomics* 92(6): 478-487. <https://doi.org/10.1016/j.ygeno.2008.07.013>
- Burr B, Evola SV, Burr FA, Beckmann JS (1983) The application of restriction fragment length polymorphism to plant breeding. *Genetic Engineering* 5: 45-59. https://doi.org/10.1007/978-1-4684-4556-5_4
- Causse M, Fulton T, Cho Y, Ahn S, Chunwongse J, Wu K (1994) Saturated molecular map of the rice genome based on an interspecific backcross population. *Genetics* 138: 1251-1274.
- Chee PW, Rong J, Williams-coplin D, Schulze SR, Paterson AH (2004) EST derived PCR-based markers for functional gene homologues in cotton. *Genome* 47: 449-462. <https://doi.org/10.1139/g04-002>
- Chen Z J, Scheffler B E, Dennis E, et al. Toward sequencing cotton (*Gossypium*) genomes. *Plant Physiol*, 2007, 145: 1303–1310. <https://doi.org/10.1104/pp.107.107672>
- Cotton: Origin, History, Technology, and Production. New York: Wiley, 1999. 33–63.
- Gupta PK, Rustgi S, Mir RR (2008) Array-based high-throughput DNA markers for crop improvement. *Heredity* (Edinb) 101: 5-18. <https://doi.org/10.1038/hdy.2008.35>
- Gutierrez OA, Basu S, Saha S, Jenkins JN, Shoemaker DB, Cheatham CL (2002) Genetic distance among selected cotton genotypes and its relationship with F2 performance. *Crop Sci.* 42: 1841-1847. <https://doi.org/10.2135/cropsci2002.1841>

- Han ZG, Guo WZ, Song XL, Zhang TZ (2004) Genetic mapping of EST-derived microsatellites from the diploid *Gossypium arboreum* in allotetraploid cotton. *Mol. Gen. Genomics* 272: 308-327. <https://doi.org/10.1007/s00438-004-1059-8>
- He DH, Lin ZX, Zhang XL, Nie YC, Guo XP, Zhang YX (2007) QTL mapping for economic traits based on a dense genetic map of cotton with PCR-based markers using the interspecific cross of *Gossypium hirsutum* x *Gossypium barbadense*. *Euphytica* 153: 181-197. <https://doi.org/10.1007/s10681-006-9254-9>
- He XH, Qin H, Hu Z, Zhang T, Zhang YM (2011) Mapping of epistatic quantitative trait loci in four-way crosses. *Theor. Appl. Genet.* 122: 33-48. <https://doi.org/10.1007/s00122-010-1420-8>
- Kohel RJ, Yu J, Park Y, Lazo GR (2001) Molecular mapping and characterization of traits controlling fibre quality in cotton. *Euphytica* 121: 163-172. <https://doi.org/10.1023/A:1012263413418>
- Kumar N, Kulwal P, Balyan H, Gupta P (2007) QTL mapping for yield and yield contributing traits in two mapping populations of bread wheat. *Mol. Breed.* 19: 163-177. <https://doi.org/10.1007/s11032-006-9056-8>
- Kumar P, Gupta VK, Misra AK, Modi DR, Pandey BK (2009) Potential of molecular markers in plant biotechnology. *Plant Omics Journal* 2(4): 141-162.
- Kumar P, Gupta VK, Misra AK, Modi DR, Pandey BK (2009) Potential of molecular markers in plant biotechnology. *Plant Omics Journal* 2(4): 141-162.
- Kumar P, Paterson AH, Chee PW (2006) Predicting intron sites by aligning cotton ESTs with Arabidopsis genomic DNA. *Journal of Cotton Science* 10: 29-38.
- Lacape JM, Jacobs J, Arioli T, Derijcker R, Forestier-Chiron N, Llewellyn D (2009) A new interspecific *Gossypium hirsutum* x *G. barbadense*, RIL population: towards a unified consensus linkage map of tetraploid cotton. *Theor. Appl. Genet.* 119: 281-292. <https://doi.org/10.1007/s00122-009-1037-y>
- Lacape JM, Llewellyn D, Jacobs J, Arioli T, Becker D, Calhoun S (2010) Meta-analysis of cotton fibre quality QTLs across diverse environments in a *Gossypium hirsutum* x *G. barbadense* RIL population. *BMC Plant Biol.* 10: 132. <https://doi.org/10.1186/1471-2229-10-132>
- Lacape JM, Nguyen TB, Courtois B, Belot JL, Giband M, Gourlot JP (2005) QTL analysis of cotton fibre quality using multiple *Gossypium hirsutum* x *Gossypium barbadense* backcross generations. *Crop Sci.* 45: 123-140. <https://doi.org/10.2135/cropsci2005.0123a>
- Lacape JM, Nguyen TB, Thibivilliers S, Bojinnov TB, Courtois B, Cantrell RG, Burr B, Hau B (2003) A combined RFLP-SSR-AFLP map of tetraploid cotton based on a *Gossypium hirsutum* · *Gossypium barbadense* backcross population. *Genome* 46:612–626. <https://doi.org/10.1139/g03-050>
- Li HB, Kilian A, Zhou MX, Wenzl P, Huttner E, Mendham N (2010) Construction of a high-density composite map and comparative mapping of segregation distortion regions in barley. *Mol Genet Genomics* 284:319-331. <https://doi.org/10.1007/s00438-010-0570-3>
- Li S, Wang J, Zhang L (2015) Inclusive composite interval mapping of QTL by environment interactions in biparental populations. *PLoS One* 10: 1-22. <https://doi.org/10.1371/journal.pone.0132414>
- Li W, Lin Z, Zhang X (2007) A novel segregation distortion in intraspecific population of Asian cotton (*Gossypium arboreum* L.) detected by molecular markers. *J. Genet. Genomics* 34: 634-640. [https://doi.org/10.1016/S1673-8527\(07\)60072-1](https://doi.org/10.1016/S1673-8527(07)60072-1)
- Liu R, Wang B, Guo W, Qin Y, Wang L, Zhang Y, Zhang T (2012) Quantitative trait loci mapping for yield and its components by using two immortalized populations of a heterotic hybrid in *Gossypium hirsutum* L. *Mol. Breed.* 29: 297-311. <https://doi.org/10.1007/s11032-011-9547-0>
- Lu H, Romero-Severson J, Bernardo R (2002) Chromosomal regions associated with segregation distortion in maize. *Theor. Applied Genet.* 105: 622-628. <https://doi.org/10.1007/s00122-002-0970-9>
- Luo L, Xu S (2003) Mapping viability loci using molecular markers. *Heredity* 90: 459-467. <https://doi.org/10.1038/sj.hdy.6800264>
- Mangelsdorf PC, Jones DF (1926) The expression of Mendelian factors in the gametophyte of maize. *Genetics* 11: 423-455.
- McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffman WR (1988) Molecular mapping of rice chromosomes. *Theor. Applied Genet.* 76: 815-829. <https://doi.org/10.1007/BF00273666>
- Mei M, Syed NH, Gao W, Thaxton PM, Smith CW, StellyDM, Chen ZJ (2004) Genetic mapping and QTL analysis of fibre-related traits in cotton (*Gossypium*). *Theor Appl Genet* 108:280–291. <https://doi.org/10.1007/s00122-003-1433-7>

- Park YH, Alabady MS, Ulloa M, Sickler B, Wilkins TA, Yu J (2005) Genetic mapping of new cotton fibre loci using EST-derived microsatellites in an interspecific recombinant inbred line cotton population. *Mol. Genet. Gen.* 274: 428-441. <https://doi.org/10.1007/s00438-005-0037-0>
- Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature* 335:721–726. <https://doi.org/10.1038/335721a0>
- Percival A, Wendel J, Stewart J. Taxonomy and germplasm resources. In: Smith C W, Cothren J T, eds.
- Pereira MG, Lee M, Bramel-Cox P, Woodman W, Doebley J, Whitkus R (1994) Construction of an RFLP in sorghum and comparative mapping in maize. *Genome* 37: 236-243. <https://doi.org/10.1139/g94-033>
- Qin HD, Guo WZ, Zhang YM, Zhang TZ (2008) QTL mapping of yield and fibre traits based on a four-way cross population in *Gossypium hirsutum* L. *Theor. Appl. Genet.* 117: 883-894. <https://doi.org/10.1007/s00122-008-0828-x>
- Qureshi SN, Saha S, Kantety RV, Jenkins JN (2004) EST-SSR: a new class of genetic markers in cotton. *The Journal of cotton science* 8: 112-123.
- Rong JK, Abbey C, Bowers JE, Brubaker CL, Chang C, Chee PW (2004) A 3347-locus genetic recombination map of sequence-tagged sites reveal features of genome organization, transmission and evolution of cotton (*Gossypium*). *Genetics* 166: 389-417. <https://doi.org/10.1534/genetics.166.1.389>
- Saha S, Karaca M, Jenkins JN, Zipf AE, Reddy OUK, Kantety RV (2003) Simple sequence repeats as useful resources to study transcribed genes of cotton. *Euphytica* 130: 355-364. <https://doi.org/10.1023/A:1023077209170>
- Shen XL, Zhang TZ, Guo WZ, Zhu XF, Zhang XY (2006) Mapping fibre and yield QTLs with main, epistatic, and QTL x environment interaction effects in recombinant inbred lines of upland cotton. *Crop Sci.* 46: 61-66. <https://doi.org/10.2135/cropsci2005.0056>
- Song X, Wang K, Guo W, Zhang J, Zhang T (2005) A comparison of genetic maps constructed from haploid and BC1 mapping populations from the same crossing between *Gossypium hirsutum* L. and *Gossypium barbadense* L. *Genome* 48: 378-390. <https://doi.org/10.1139/g04-126>
- Sun FD, Zhang JH, Wang SF, Gong WK, Shi YZ, Liu AY (2012) QTL mapping for fibre quality traits across multiple generations and environments in upland cotton. *Mol. Breed.* 30: 569-582. <https://doi.org/10.1007/s11032-011-9645-z>
- Tanksley SD, Miller JC, Paterson AH, Bernatzky R (1988) Molecular mapping of plant chromosomes. *Chromosome structure and function* 157-172. https://doi.org/10.1007/978-1-4613-1037-2_7
- Taylor DR, Ingvarsson PK (2003) Common features of segregation distortion in plants and animals. *Genetica* 117: 27-35. <https://doi.org/10.1023/A:1022308414864>
- Ulloa M, Meredith WR, Shapplet ZW, Kahler AL (2002) RFLP genetic linkage maps from four F2:3 population and a joinmap of *Gossypium hirsutum* L. *Theor Appl Genet* 104:200–208. <https://doi.org/10.1007/s001220100739>
- Ulloa M, Saha S, Jenkins JN, Meredith Jr WR, McCarty Jr JC, Stelly DM (2005) Chromosomal assignment of RFLP linkage groups harboring important QTLs on an intraspecific cotton (*Gossypium hirsutum* L.) joinmap. *J. Hered.* 96: 132-144. <https://doi.org/10.1093/jhered/esi020>
- Van Esbroeck GA, Bowman DT, Calhoun DS, May OL (1998) Changes in the genetic diversity of cotton in the U.S. from 1970 to 1995. *Crop Sci.* 38: 33-37. <https://doi.org/10.2135/cropsci1998.0011183X003800010006x>
- Wang K, Song XL, Han ZG, Guo WZ, Yu JZ, Sun J, PanJJ, Kohel RJ, Zhang TZ (2006) Complete assignment of the chromosomes of *Gossypium hirsutum* L. by translocation and fluorescence in situ hybridization mapping. *Theor Appl Genet* 113:73–80. <https://doi.org/10.1007/s00122-006-0273-7>
- Wendel JF, Brubaker CL, Percival AE (1992) Genetic diversity in *Gossypium hirsutum* and the origin of upland cotton. *Am. J. Bot.* 79: 1291-1310. <https://doi.org/10.1002/j.1537-2197.1992.tb13734.x>
- Wu J, Gutierrez OA, Jenkins JN, McCarty JC, Zhu J (2009) Quantitative analysis and QTL mapping for agronomic and fibre traits in an RI population of upland cotton. *Euphytica* 165: 231- <https://doi.org/10.1007/s10681-008-9748-8>
- Xu Y, Crouch JH (2008) Marker-assisted selection in plant breeding from publications to practice. *Crop Sci.* 48: 391. <https://doi.org/10.2135/cropsci2007.04.0191>
- Yu J, Zhang K, Li S, Yu S, Zhai H, Wu M (2013) Mapping quantitative trait loci for lint yield and fibre quality across environments in a *Gossypium hirsutum* x *Gossypium barbadense* backcross inbred line population. *Theor. Appl. Genet.* 126: 275-287. <https://doi.org/10.1007/s00122-012-1980-x>

- Yu JZ, Kohel RJ, Fang DD, Cho J, Van Deynze A, Ulloa M (2012) A high-density simple sequence repeat and single nucleotide polymorphism genetic map of the tetraploid cotton genome. *Genes Genomes Genet.* 2: 43-58. <https://doi.org/10.1534/g3.111.001552>
- Yu Y, Yuan DJ, Liang SG, Li XM, Wang XQ, Lin ZX (2011) Genome structure of cotton revealed by a genome-wide SSR genetic map constructed from a BC1 population between *Gossypium hirsutum* and *G. barbadense*. *BMC Genomics* 12:15. <https://doi.org/10.1186/1471-2164-12-15>
- Zhang K, Zhang J, Ma J, Tang S, Liu D, Teng Z (2012) Genetic mapping and quantitative trait locus analysis of fibre quality traits using a three-parent composite population in upland cotton (*Gossypium hirsutum* L.) *Mol. Breed.* 29: 3350348. <https://doi.org/10.1007/s11032-011-9549-y>
- Zhang L, Li H, Ding J, Wu J, Wang J (2015) Quantitative trait locus mapping with background control in genetic populations of clonal F1 and double cross. *J. Integr. Plant Biol.* 57: 1046-1062. <https://doi.org/10.1111/jipb.12361>
- Zhang ZS, Hu MC, Zhang J, Liu DJ, Zheng J, Zhang K (2009) Construction of a comprehensive PCR-based marker linkage map and QTL mapping for fibre quality traits in upland cotton (*Gossypium hirsutum* L.) *Mol. Breed.* 24: 49-61. <https://doi.org/10.1007/s11032-009-9271-1>
- Zhang ZS, XiaoYH, Luo M, Li XB, Luo XY, Hou L. (2005) Construction of a genetic linkage map and QTL analysis of fibre-related traits in upland cotton (*Gossypium hirsutum* L.) *Euphytica* 144: 91-99. <https://doi.org/10.1007/s10681-005-4629-x>
- Zhao L, Lv Y, Cai C, Tong X, Chen X, Zhang W (2012) Toward allotetraploid cotton genome assembly: integration of a high-density molecular genetic linkage map with DNA sequence information. *BMC Genomics* 13: 539. <https://doi.org/10.1186/1471-2164-13-539>
- Zhu C, Wang C, Zhang YM (2007) Modeling segregation distortion for viability selection. I. Reconstruction of linkage maps with distorted markers. *Theor. Appl. Genet.* 114: 295-305. <https://doi.org/10.1007/s00122-006-0432-x>